# PHOTOTAXIS IN VOLVOX.

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The reactions of *Volvox* to light have been studied in some detail by Oltmanns[1] who came to the conclusion that the phototactic movements of this organism are determined through the effort to reach a region of a certain optimum intensity of illumination. The theory at which Sachs and Strasburger had arrived from their studies of the phototactic reactions of plants, and which Loeb had applied to the phototaxis of animals, namely, that the direction of the movement is determined by the direction of the rays of light is not accepted by Oltmanns, but the experiments upon which this writer bases his confutation of this theory do not, I believe, bear out his interpretation. Oltmanns studied the reactions of *Volvox* to light of varying intensity by keeping specimens in a vessel so illuminated that the intensity of light gradually increased from one end to the other. This was accomplished by covering the vessel with a box the top and ends of which were made of wood while the sides were formed of narrow, wedge-shaped, hollow glass prisms filled with a mixture of India-ink and gelatine. The small ends of the prisms allowed most of the light to pass through, while the thick ends absorbed most of the rays. The light entering the enclosed vessel was obviously greatest opposite the thin ends of the prisms and gradually diminished toward the opposite end. The *Volvox* were found to assemble in different places in the vessel according to the intensity of light which fell upon the lateral prisms. With a comparatively dim outside light they would gather in the brightest end of the vessel; in light of very strong intensity they would seek the darkest end; while with moderate illumination they would take up some intermediate position. These results were held by Oltmanns to indicate that the *Volvox* seek the places of optimum intensity of illumination and remain there,

[1] Flora, 1892, p. 183.

much as higher organisms collect in situations where it is neither too warm nor too cold. In the experiments of Oltmanns we certainly cannot assume that the factor of the direction of the rays has been excluded. Owing to the scattering of the rays entering perpendicularly through the sides the light end of the vessel, in such an apparatus as Oltmanns employed, must act practically as an independent source of light. If, therefore, *Volvox* is positively phototactic in weak light and negatively so in strong, we may readily understand why collections are formed in regions of a certain intensity of illumination in accordance with the theory that the direction of movements is determined by the direction of the rays.

As an opportunity presented itself this last fall of procuring *Volvox* easily and in large numbers I endeavored to work out some points in the phototaxis of this organism a little more in detail, and, if orientation to the direction of the rays should be found to occur, as seemed probable from the statement of previous observers, to ascertain the method by which the orienting response is brought about. It is easy to determine that *Volvox* orients itself, and that very accurately, to the direction of the rays of light. If specimens of *Volvox* are taken into a dark room and exposed to the light from an arc lamp they travel towards the light in almost a straight course, swerving remarkably little to the one side or the other. They will often travel a foot without deviating as much as a quarter of an inch from a perfectly straight course. If the position of the light is changed during their progress they soon re-orient themselves and travel straight onwards as before. If the light is placed at the other end of the vessel they turn about and come back to where they started. The shape of the *Volvox* is not quite spherical but slightly elongated, forming a prolate spheroid, and when swimming through the water the organism rotates on its long axis. As is well known the anterior end of *Volvox* may be distinguished by the fact that it is usually free from daughter colonies, and Ryder has pointed out that the red ocelli of the zoöids are much larger at this end than elsewhere and diminish gradually in size towards the posterior end of the body. While swimming towards the light the largest ocelli are always directed towards the region of greatest illumination.

That *Volvox* is negatively phototactic in strong light may be determined by exposing it to direct sunlight, or to a beam from a projection lantern after eliminating the heat rays by means of an alum cell. In negative phototaxis the body is also definitely oriented, but with the anterior end away from the light, and the organism swims away in a very nearly straight course. When it reaches a place where the light becomes less than the optimum it stops and remains comparatively quiet, only moving about slowly at intervals in an irregular manner. In very weak light *Volvox* exhibits no pronounced phototactic movements, but either lies quiet or rolls about sluggisly in various directions. With stronger illumination it becomes more active and swims straight towards the source of light, while in light of high intensity the direction of the response is reversed. We may readily understand, therefore, why in the experiments of Oltmanns the *Volvox* formed groups in regions of a certain intensity of illumination. Collections would be formed if the *Volvox* moved about irregularly without regard to the direction of the rays and came to rest when they reached a region of a particular intensity of light; but it is clear that this is not the method pursued. There are few organisms in which the orientation to the direction of the rays is more precise, or which travel to or from the light in more nearly a straight line.

How is the orientation of *Volvox* effected? It is practically impossible to determine this by studying the movements of the flagella of the individual cells, as any one who has attempted to observe these movements will easily realize. We are safe in saying that when *Volvox* changes its direction it is because the flagella on the two sides of the organism beat unequally. Can we explain the orientation, then, as a result of the fact that the differences of intensity of light on the two sides of the body cause the flagella to beat with unequal vigor so that the organism is swung around into a position of equal bilateral stimulation? It is in this way that Holt and Lee[1] have attempted to explain the orientation of *Volvox*, but there are certain difficulties in the way of such an interpretation. Let us consider a *Volvox* in a region of suboptimal stimulation and lying obliquely to the rays

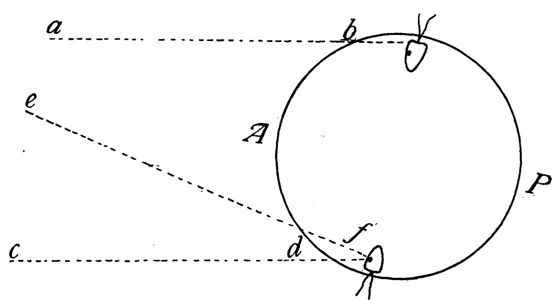
[1] *American Journal of Physiology*, Vol. IV.

of light. If it orients itself to the light the backward stroke of the flagella, *i. e.* the stroke that is effective in propelling the body forward must be more effective on the shaded side than on the brighter side. This may conceivably occur in the following ways, which, however, amount practically to the same thing: The diminished intensity of light on the shaded side of the body may act as a stimulus to the backward phase, or decrease the efficiency of the forward phase of the stroke of the flagella; or the light on the brighter side of the body may inhibit the backward phase, or increase the forward phase of the stroke of the flagella. In any case, if the organism is passing into regions of ever-increasing intensity of light, we should expect its rate of speed would be lowered. If the orientation is effected by a shading of the side away from the light it would follow that in a region in which the shading were less the speed of the travelling body would be diminished. If the parts of the body which are most shaded are the parts where the effective beat of the flagella is the strongest, then, as the organism passes to a point where the illumination on both sides of its body is increased, its rate of transit would be diminished. If we suppose that the forward stroke is most stimulated, or the backward stroke most inhibited on the brightest side of the body we should expect that with more illumination the more inhibition there would be, or the more the backward phase of the stroke would be increased, and the rate of locomotion would likewise be reduced. If we imagine a machine in the form of a *Volvox* colony and provided on all sides with small movable paddles so adjusted that when they came into regions of diminished light as the machine rolled through the water their effective beat would be increased, it is clear that such a machine might orient itself to the direction of the rays and travel towards the source of illumination, but its rate of locomotion would be diminished the brighter the light into which it passed. We may conceive the light to increase or decrease the backward or forward stroke of the paddles in any way we please and we cannot explain how such a machine can orient itself and go towards the light and at the same time move through the water more rapidly as it comes into regions of greater illumination.

Does *Volvox* react to light as the theory above mentioned would lead us to expect? Oltmanns' observation on the relation of the rate of movement of *Volvox* to the intensity of illumination, while they apparently do not conform to this theory, were not made sufficiently in detail to form a crucial test of its validity. In order to obtain evidence which would be somewhat more conclusive I placed specimens of *Volvox* in a narrow glass trough through one end of which light from an arc lamp was passed after having filtered through an alum cell. The trough was placed over a paper ruled off in spaces a centimeter in width. The specimens were placed at such a distance as was found by previous trials was about the point where they would begin to orient themselves and travel towards the light. The number of seconds required by a specimen to travel across successive intervals in its passage towards the light was noted. The experiment was repeated many times, both by using different specimens and by using the same one over again. It was found that, as the *Volvox* travelled towards the light, their movement was at first slow, their orientation not precise, and their course crooked. Gradually their path became straighter, the orientation to the light rays more exact and their speed more rapid. After travelling over a few spaces, however, their speed became remarkably uniform until the end of the trough was reached where they would remain. If the light is so intense that one end of the trough is above the optimum intensity of illumination the speed of the *Volvox* is decreased as it approaches this optimum where it finally stops. In going away from very intense light *Volvox* moves at a nearly uniform rate until within a few centimeters of the optimum when the speed begins to diminish. There is thus a lessening of speed as the optimum is approached from either direction. The distance over which there is either a marked increase or decrease of speed is considerably less, however, than the space over which the speed is nearly uniform.

When we attempt to explain the foregoing facts on the theory that orientation is effected through the differences of the intensity of light on the two sides of the organism we inevitably get into difficulties. If the *Volvox* acts as a lens concentrating the rays on the side farthest from the light so that that side is more intensely illuminated the behavior of the organism would meet the requirements of the theory. Orientation, however, occurs, apparently equally well, in those individuals which contain so many daughter colonies that a large proportion of the light is intercepted in passing through the organism ; this explanation must, therefore, be dismissed even if it be otherwise valid. How then is the orientation of *Volvox* brought about ? This problem is one rather more difficult to solve than it might seem. There is a suggestive similarity between the phototaxis of *Volvox* and the reactions of this organism to the electric current. Carlgren has found that *Volvox* orients itself very precisely to the constant current and swims in very nearly a straight path to the kathode. After a prolonged action of the current a more or less pronounced tendency to go towards the anode asserts itself, but the latter form of electrotaxis is much less precise and characteristic. It seems not altogether improbable that light in passing through a nearly transparent organism like *Volvox* exercises a directive effect upon its movements in a similar way, whatever it may be, to that produced by the current of electricity. The direction of the rays may be the important factor in orientation irrespective of differences of intensity of light upon different parts of the organism as has been maintained by Sachs for the phototropic movements of plants. I am not ready to adopt the theory of Sachs, but I feel that it is a view that is not entirely out of court.

There is one feature of the structure of *Volvox* which may be of some significance in relation to the problem of orientation. As Overton has pointed out, the red eye spots of the cells are so placed that they all face the anterior end of the colony. When this end is directed toward the light the spots are in a position to receive more than the usual stimulus. Orientation of the colony would be produced if each cell were to react in such a manner as to cause the eye spot to face the light. We have little direct evidence, aside from a single experiment of Englemann on *Euglena*, that the so-called eye spots of the Flagellata are photorecipient organs, but there are certain facts regarding the occurrence of these spots as well as their arrangement in *Volvox* which render it probable that such is their function. We may conceive that each cell of the colony tends to orient itself at a different angle to the rays of light, the cells of the anterior end where the largest eye spots occur placing themselves with their long axes parallel with the rays, and the other cells at various angles depending upon their position in the colony. To account for the orientation of the colony we are thrown back upon the problem of the mechanism of the process whereby each individual cell places itself so that its eye spot faces the source of light. The behavior of the cells of the colony, according to this interpretation would fall into Prof. Mark Baldwin's somewhat extensive category of imitative activity, in that each cell reacts so as to secure more of the stimulus affecting a specialized portion of its structure. How and why the cells so react we still have to explain, and various theories of orientation may be applied to the individual cells. The orientation of the colony may be accounted




for rather more simply, however, if we suppose that the eye spots are most sensitive to light striking them at a certain angle such as is indicated in the diagram by the lines *ab* and *ef*. If rays of light enter the colony in the direction of the lines *ab* and *ef* somewhat obliquely to the long axis, *AP*, the flagella of the cell represented on the upper side of the diagram would beat more vigorously and accelerate the motion of that side of the organism. The opposite cell being struck by rays in the direction *cd* would be less stimulated, and, as the flagella would beat less strongly than those on the other side of the colony, the organism would swing about until its long axis is brought parallel with the rays when, being equally stimulated on both sides, it would move in a straight course towards the light. We do not have to suppose that each cell makes a special effort to orient itself at a particular angle to the rays, but that it is so organized that the effective beat of its flagella is most accelerated by light striking the cell at a certain angle. If the cells were most stimulated by light falling upon them at such an angle as would result if the rays diverged from a spot in front of the colony and in line with its long axis the conditions for orientation would be fulfilled. Since the eye spots in all the cells face the anterior end of the colony this supposition appears very probable. The foregoing explanation of the orientation of *Volvox* may or may not be the true one, but it enables us to see a significance in the peculiar arrangement of the eye spots in this form and is consistent with the results of the experiments we have described.

How are we to explain the fact that *Volvox* becomes negatively phototactic in light of strong intensity? We certainly cannot explain the reversal on the supposition that it is due to a difference of emphasis in the phases of the stroke of the flagella. In positive phototaxis the backward phase of the stroke of the flagella is the stronger, and if we suppose that with increase of stimulation the reverse phase comes to predominate the organism would go backwards instead of forwards. As it is the anterior end of the organism that is directed away from the light in negative phototaxis it is obvious that the same phase of the stroke of the flagella predominates is both cases. The theory of Holt and Lee applies here very well; if the effective beat of the flagella is greatest on the more illuminated side the organism would naturally turn about so as to point away from the light. This may or may not be the true explanation of the negative reaction; I see at present no way either of proving or of disproving it. The probability of the supposition is somewhat weakened, however, by the fact that it cannot also be applied to positive phototaxis. It seems probable that light accelerates the action of the flagella not only by stimulating the eye spots but by acting on other parts of the cells, and we might suppose that, as the light is increased, a point would be reached where the stimulus to the other parts of the cell would outweigh the effect upon the eye spots, and the flagella on the side of the organism nearest the light, beating more vigorously than the others, would thereby bring about the negative orientation. We can thus give at least a formal explanation of the phenomenon. There are many instances in which an increase in the intensity of a stimulus causes a reversal of the usual reaction, but the reason for this in any case is still an unsolved problem.